

USING GENETIC RELATEDNESS TO INVESTIGATE THE DEVELOPMENT OF CONFLICT BEHAVIOR IN BLACK BEARS

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The acquisition of behavior in animals is a function of both inheritance and learning, where learning can occur asocially (independent of other animals), socially (by observing other animals), or both. For species that have a prolonged parent–offspring relationship and that live solitary adult lives, social learning between parents and offspring may be a dominant form of learning. If parent–offspring learning is a dominant avenue for acquiring behavior or if behavior is inherited, then behaviors that confer significant fitness advantages should lead to subpopulations of genetically related individuals with similar behavioral patterns. We investigated whether food-conditioning behavior in black bears (*Ursus americanus*) is inherited or learned via parent–offspring social learning. We combined genetic data with behavioral data for 116 black bears from Lake Tahoe Basin, Nevada, and Yosemite National Park, California. We categorized individual bears as food-conditioned or non-food-conditioned based on their behavior over a several-year period of intensive study at each site. We compared levels of relatedness, based on microsatellite DNA genotyping, within and between these groups and compared behavior between 9 mother–offspring pairs determined through genetic analysis of maternity. Based on 4 separate analyses of the data there was little evidence that food-conditioning behavior in black bears partitioned along related lineages, indicating that the acquisition of food conditioning behavior was not solely a function of social learning or inheritance.

Key words: asocial learning, black bear, food conditioning, F_{ST} , Lake Tahoe Basin, microsatellite, relatedness, social learning, *Ursus americanus*, Yosemite National Park

For all animals the acquisition of behavior (e.g., acquired dietary preferences, techniques of foraging, travel routes, and mate choice) is critical for survival and reproduction (Domjan 1998; Shettleworth 1998). Some behavioral traits are acquired primarily via inheritance, but for many animals the acquisition of most behavior is at least partially dependent upon learning (Box and Gibson 1999; Heyes and Galef 1996). Learning can occur via 2 general mechanisms, asocial learning where an individual learns independently or social learning where an individual is influenced by observation of others (Galef 1988; Heyes 1994). The relative importance of social compared to

asocial learning for most free-ranging species is poorly understood (Galef and Giraldeau 2001; Galef and Whiskin 2001), primarily because of the difficulties of studying learning in the field (Galef 2004).

Understanding how animals acquire behavior is an important goal for both basic (e.g., evolutionary biology) and applied (e.g., conservation biology and wildlife management) scientific disciplines. For example, wildlife managers are increasingly using nonlethal tools such as aversive conditioning that focus on altering the behavior of individual animals to solve human–carnivore conflicts (Breck 2004). Understanding how animals acquire behavior is critical for resolving such conflicts. Laboratory experiments have demonstrated that some species learn novel skills and information more quickly through social learning than asocial learning (Galef and Giraldeau 2001; Galef and Laland 2005; Palameta and Lefebvre 1985). However, laboratory studies do not provide much insight into the nature of learning in free-ranging animals (Fragaszy and Visalberghi

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2001; Gajdon et al. 2004; Galef 1996). Galef (2004) advocated more experimentation in field settings to gain insight about the role of social learning in free-ranging populations. But for most species there are few opportunities to implement experiments in the field; therefore, developing techniques for investigating the role of social and asocial learning in free-ranging animals is important (Fragaszy and Visalberghi 2001).

Species that have prolonged juvenile–parent relationships and then live relatively solitary adult lives offer opportunities to understand the relative roles of social and asocial learning because of the potential to categorize and compare measures of behavior and relatedness among individuals. Our logic is based on the idea that in solitary species the primary opportunity for social learning exists between parent and offspring (Gilbert 1999). If a particular behavior is passed between parent and offspring, either by inheritance or through social learning, then this should lead to genetically related individuals that are identifiable by their behavior (unless other factors mask the expression of the behavior). Alternatively, if social learning occurs between unrelated individuals or if individuals in a population learn via asocial mechanisms, then the link between related individuals and a unique behavior will be weak, providing evidence that other mechanisms for learning are important.

Black bears (*Ursus americanus*) are good candidates for studying whether particular behaviors are passed between parent and offspring because black bears are highly solitary throughout their life with exceptions being the prolonged mother–offspring relationship, occasional congregations at feeding sites, and a few weeks of sociality between adult males and females during the breeding season (Pelton 2003). Little is known about asocial or social learning in free-ranging populations of black bears (Gilbert 1999), but based on their life history it is reasonable to assume that most social learning occurs during the 16–18 months that cubs remain with their mother and that acquisition of a behavior that conferred significant fitness advantages could be transferred through this mother–offspring relationship.

The development of feeding strategies based on the consumption of human-based food (i.e., food conditioning) is a behavior that can confer significant advantages for individual black bears (Beckmann and Berger 2003; Gilbert 1999). Bears that exhibit this type of behavior show increased weight gain, increased reproduction, decreased home-range sizes, and alterations in their activity periods (Beckmann and Berger 2003; Matthews et al. 2006), all of which indicate fitness advantages to individuals that acquire this behavior. Development of food-conditioned (FC) behavior can also create alternative causes of mortality for bears (e.g., collisions with cars). However, it is unlikely that these mortality factors prevent recruitment and opportunity for behavior to be passed between generations. Biologists that manage conflicts between bears and humans often speculate that bears exhibiting conflict behavior acquire it from their mothers, implying that parent–offspring learning, genetic inheritance, or both play a strong role in the development of food-conditioning behavior (S. W. Breck, pers. comm.). Meagher and Fowler (1989) suggested that the maintenance of “problematic” feeding behavior of

grizzly bears (*Ursus arctos*) in Yellowstone National Park was a function of behavior being passed from mother to offspring. They reported evidence demonstrating that female brown bears that exhibited this behavior were from related lineages spanning successive generations.

In this study, we investigated whether 2 distinct behavioral patterns, non–food-conditioned (NFC) and FC, observed in populations of black bears were partitioned along genetic lineages. We used data from 2 separate bear populations where both NFC and FC bears were studied, and used behavioral and genetic data to compare genetic relatedness within and between NFC and FC bears. If behavior between individuals was similar because of genetic inheritance or parent–offspring social learning, then we expected to see concordant behavioral and genetic divisions (e.g., along familial lineages), akin to the suggestion of lasting divisions between “dump” and “wild” bears (Stringham 1989).

MATERIALS AND METHODS

We determined behavioral patterns of black bears from 2 distinct populations, 1 in Nevada (Lake Tahoe Basin and Carson Front [LTB]) and 1 in California (Yosemite National Park [YNP]). Bears from LTB were restricted to an area of approximately 3,800 km² in western portions of Nevada within the Lake Tahoe Basin and the Carson Front. YNP is located on the western slope of the Sierra Nevada Mountains in east-central California, encompassing more than 3,080 km² (Graber and White 1983). Observations of bears at both areas revealed 2 distinct behavior patterns among bears at each study area; NFC bears rarely if ever exhibited behavior that was in conflict with humans and FC bears were frequently involved in conflict with humans, including consuming anthropogenic food, causing property damage, and entering occupied buildings (Beckmann and Berger 2003; Beckmann and Lackey 2004; Hastings et al. 1989; Matthews et al. 2006).

We categorized bears ($n = 57$ from LTB and $n = 46$ from YNP) as NFC or FC based on direct observations of activity patterns, movements, and foraging behavior (Beckmann and Berger 2003; Matthews et al. 2006). Details of methodology and behavioral results were previously presented (Beckmann and Berger 2003; Matthews et al. 2006), but generally bears were studied using radiotelemetry and repeated observations over a 3- to 4-year period. Individuals were classified as either NFC or FC based on direct observation and on whether or not they used anthropogenic food and garbage. With few exceptions, individuals were easily classified in either category and remained in that category for the duration of study. Although behavior can be considered a continuous variable, we used discrete behavioral categories because the data from each study indicated a clear distinction between NFC and FC bears.

We collected genetic material only from bears that were captured with Aldrich spring-activated snares (Aldrich Spring Activated Animal Snare, Aldrich, Callum Bay, Washington), culvert traps, or free-ranging techniques (capture of an unconfined animal using chemical immobilization darts filled with an immobilization agent and shot with an air rifle). Blood

was collected from all bears from YNP and stored in BD Vacutainer K2 EDTA blood collection tubes (BD, Franklin Lakes, New Jersey). Hair samples were taken from bears from LTB using forceps to pluck hair with the roots intact. The hair was then stored in sample envelopes in a freezer. All animals were handled in a humane manner that followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by an institutional animal care and use committee (see Beckmann and Berger 2003; Matthews et al. 2006). In addition to the bears described above, hair samples were collected from 13 additional bears from LTB, but because of time and funding constraints they were not assigned to behavioral categories (genetic samples from LTB, $n = 70$). DNA was isolated using a DNEasy kit (Qiagen, Valencia, California). Bears were genotyped at 9 microsatellite loci (CXX20 [Ostrander et al. 1993]; G1A, G1D, G10B, G10C, G10L, and G10X [Paetkau et al. 1995]; and G10O and G10P [Paetkau et al. 1998]). YNP bears were also genotyped at 2 additional loci (G10H and G10J—Paetkau et al. 1998) because of greater yields of DNA from blood. One primer of each pair was fluorescently labeled and genotypes were determined using an ABI PRISM 377 automated DNA sequencer equipped with Genescan and Genotyper software (Applied Biosystems, Foster City, California). Hair samples were handled in laboratory areas with equipment dedicated to noninvasive samples and genotyped 4 times at each locus to reduce genotyping errors. We extracted DNA from the roots of 5–10 hairs, as available, and initially performed amplifications in quadruplicate. Alleles were scored if they were detected at least twice. Samples that resulted in homozygous genotypes were amplified and scored an additional 1–3 times at those loci. All samples produced consensus genotypes that met our criteria.

We analyzed bears within each study site separately. For each study site, the average number of alleles per locus and expected and observed heterozygosity were calculated using the software package Genetic Data Analysis (Lewis and Zaykin 1999). We also calculated an estimate of the level of variance partitioning, F_{ST} , between NFC and FC bears at each site, and estimated statistical significance via bootstrap analysis using 95% confidence intervals over 1,000 replicates, using Genetic Data Analysis. We calculated the probability of identity for siblings over all loci within each population using the software package API-CALC (Ayres and Overall 2004). We calculated pairwise relatedness (r) between individuals within study areas using Relatedness (version 5.0—Queller and Goodnight 1989). Theoretical values of r range from -1 to 1 , with negative values indicating unrelated pairs and increasing r -values corresponding to increased relatedness. Based on r -values from known mother–offspring ($n = 3$) and sibling ($n = 2$) pairs, we used a value of $r \geq 0.445$ to indicate a pair related at the level of 1st-order relatives (parent–offspring or sibling pairs, which we refer to as close relatives). This is very similar to the theoretically expected value of 0.5 for 1st-order relatives (parent–offspring pairs and sibling pairs).

We performed 4 different analyses to test whether NFC bears were genetically differentiated from FC bears. First, we used F_{ST} values to test for reproductive isolation between NFC and

FC bears. Theoretical F_{ST} values range from 0 to 1 , with 0 indicating no differentiation and 1 indicating complete differentiation among populations. Thus, if NFC and FC bears partitioned among groups then values of F_{ST} would be large and statistically significant (based on bootstrap analysis using 95% confidence intervals over 1,000 replicates).

Second, we classified all pairs of 1st-order relatives as being within-group related pairs (FC–FC and NFC–NFC) or between-group related pairs (FC–NFC). We used either a chi-square goodness-of-fit test or Fisher's exact test (when sample size in at least 1 category was ≤ 5) to determine if the number of observed related pairs differed from the number of expected within each behavioral group. Expected numbers were calculated as the total number of within-group pairs multiplied by the proportion of all possible pairings within a category.

Third, we assigned mothers to cubs using Cervus 2.0 (Marshall et al. 1998). We used age estimates from analysis of cementum (Matson's Laboratory, LLC, Milltown, Montana) and known mortality dates to identify potential maternal relationships. Bears were considered potential mothers if they were estimated to be ≥ 3 years older than the bear presumed to be the offspring. Maternity was assigned to each bear individually using its own set of potential candidate mothers and allele frequencies from its population. Based on individual genotypes and population allele frequencies, Cervus 2.0 (Marshall et al. 1998) created a list of likely parents in order of decreasing likelihood and attached a statistical confidence to those assignments. Mothers were assigned if there were no genotype incompatibilities and if assignments were made with $\geq 80\%$ confidence.

Finally, we used r -values from all possible pairings of bears as a continuous variable (ranging from -1 to 1) and categorized pairs into 3 groups (FC–FC, NFC–FC, or NFC–NFC). We generated mean r -values for each group and tested for differences using an analysis of variance (ANOVA). We also performed a Duncan's multiple range test to determine where differences in means occurred (SAS PROC GLM—SAS Institute Inc. 1999). If behavior partitioned along genetically related lineages then we expected the mean r -values of within-group related pairs (i.e., FC–FC and NFC–NFC) to be greater than mean r -values of between-group related pairs (NFC–FC). We also tested for differences in the cumulative frequency distributions between the 3 groupings using the Kolmogorov–Smirnov 2-sample test (Sokal and Rohlf 1981).

RESULTS

Lake Tahoe Basin.—For the 57 bears that could be categorized based on behavioral data, 41 were FC (14 females and 27 males) and 16 were NFC (7 females and 9 males). Seventy bears were included in the genetic analyses. Hair samples from 50 bears yielded genotypes at all 9 loci, samples from 13, 6, and 1 bear yielded genotypes at 8, 7, and 6 loci, respectively. The average number of alleles per locus in bears from LTB was 4.6, with a range of 2–8. The observed multi-locus heterozygosity (0.465) was close to expected (0.495). The probability of identity for siblings was 6.93×10^{-3} . F_{ST}

TABLE 1.—Mean r-values from all possible pairings of black bears (*Ursus americanus*) labeled as either food conditioned (FC) or non-food conditioned (NFC) at 2 study sites, Lake Tahoe Basin and Yosemite National Park. Pairs were categorized as either within related pairs (NFC–NFC or FC–FC) or between related pairs (NFC–FC). Duncan groupings represent results of the Duncan's multiple range test and reveal which pairings had mean r-values significantly different from other pairings.

Behavioral groupings	Tahoe			Yosemite		
	r-values ($\bar{X} \pm SE$)	Duncan grouping	n	r-values ($\bar{X} \pm SE$)	Duncan grouping	n
NFC–NFC	-0.017 ± 0.027	A	120	-0.049 ± 0.021	B	171
FC–FC	0.047 ± 0.011	B	820	0.034 ± 0.015	A	351
NFC–FC	-0.027 ± 0.012	AB	656	-0.025 ± 0.012	B	513

between FC and NFC bears was small (0.007) and not statistically significant. The number of close relatives per bear within LTB ranged from 0 to 12. Of the 7 bears from LTB without close relatives in either category, 6 were males (5 FC and 1 NFC) and 1 was an FC female. Observed numbers of within-group pairs of bears that were 1st-order relatives ($n = 49$ for FC–FC pairs and $n = 13$ for NFC–NFC pairs) did not differ from the number expected by chance (Fisher's exact test, $P = 0.3384$). Observed numbers of between-group 1st-order related pairs (FC–NFC) also did not differ from those expected by chance ($\chi^2 = 4.370$, $df. = 3$, $P = 0.224$). Mothers were identified for 6 bears. The 4 FC mothers had in total 2 NFC cubs (1 female and 1 male) and 2 FC cubs (both male). The 2 NFC mothers had 2 FC cubs (1 female and 1 male). The differences in mean r-values between behavioral groupings were small (Table 1), with mean values ranging from -0.017 to 0.047 . Results from the ANOVA were marginally significant ($F = 2.62$, $df. = 2$, $P = 0.073$, $n = 1,595$) and the Duncan's multiple range test indicated that FC–FC grouping had mean r-values greater than NFC–NFC (Table 1). The Kolmogorov–Smirnov tests indicated there were no differences in the cumulative frequency distribution of r-values between any of the behavioral categories (FC–FC versus NFC–FC: $ks = 0.850$, $P = 0.472$; FC–FC versus NFC–NFC: $ks = 0.957$, $P = 0.298$; NFC–NFC versus NFC–FC: $ks = 0.883$, $P = 0.420$; Fig. 1).

Yosemite National Park.—For the 46 bears from YNP that we classified based on behavioral data, 27 were FC (14 females and 13 males) and 19 were NFC (7 females and 12 males). The average number of alleles per locus in bears from YNP was 3.8, with a range of 2–5. The observed multilocus heterozygosity (0.450) was close to expected (0.488). The probability of identity for siblings was 1.43×10^{-3} . The F_{ST} between FC and NFC bears was small (0.009) and not statistically significant. The number of close relatives per bear ranged from 0 to 5. Of the 8 bears from YNP without close relatives in either category, 5 were males (2 FC and 3 NFC) and 3 were females (1 FC and 2 NFC). Observed numbers of within-group bear pairs that were 1st-order relatives ($n = 24$ for FC–FC pairs and $n = 4$ for NFC–NFC pairs) did not differ from the number expected (Fisher's exact test, $P = 0.121$). Observed numbers of between-group 1st-order related pairs (FC–NFC) also did not differ from expected ($\chi^2 = 4.073$, $df. = 3$, $P = 0.254$). Mothers were identified for 3 bears. The 2 FC mothers had 1 NFC cub (male) and 1 FC cub (female). The NFC mother had 1 male NFC cub. Similar to LTB, differences of mean r-values between

behavioral groupings were small (Table 1) with mean values ranging from -0.049 to 0.034 . The ANOVA indicated a highly significant difference in mean values of relatedness between categories of behavior ($F = 7.19$, $df. = 2$, $P < 0.001$, $n = 1,035$) and the Duncan's multiple range test indicated FC–FC bears had mean r-values greater than NFC–FC and NFC–NFC bears (Table 1). The Kolmogorov–Smirnov tests also indicated that the cumulative frequency distribution of r-values differed between FC–FC and the other 2 categories (FC–FC versus NFC–FC: $ks = 1.732$, $P = 0.005$; FC–FC versus NFC–NFC: $ks = 1.307$, $P = 0.066$; NFC–NFC versus NFC–FC: $ks = 0.750$, $P = 0.648$; Fig. 1).

DISCUSSION

Results of the first 3 analyses at both study areas were similar; food-conditioning behavior in black bears showed little evidence of partitioning along genetically related lineages. First, at both study sites we found F_{ST} values were small between FC and NFC bears, indicating a lack of genetic divergence between the 2 groups (i.e., high gene flow, leading to a similar distribution of allele frequencies). Second, if FC and NFC bears separated along lineages, we would have detected differences in the numbers of 1st-order relatives categorized as within-group and between-group related pairs, but we found no evidence of this in either population. Third, from both populations we identified mothers for 9 bears, 5 (56%) of which did not share behavioral categories with their mothers. Although sample sizes were small, this was the most direct evidence that maternal behavior was not an accurate predictor of offspring behavior.

In the 4th analysis we did detect a statistical difference in mean r-values between groupings of bears especially in the population of bears from YNP (Table 1). Of note was the consistent pattern of the largest mean r-value for the FC–FC category and the smallest value for the NFC–NFC category for both LTB and YNP (Table 1). The Kolmogorov–Smirnov tests supported the ANOVA, indicating that especially in YNP, bears paired as FC–FC had a cumulative frequency distribution different than the other categories of pairings. Visual inspection of Fig. 1 reveals that all categories had a normal distribution of r-values and that the FC–FC distribution was shifted to the right relative to the other 2 distributions as opposed to a different distribution pattern (e.g., bimodal). These results are

suggestive that FC bears are passing on food-conditioning behavior to related individuals.

However, we argue that results from the 4th analysis do not constitute strong evidence that food-conditioning behavior partitions along genetically related lineages. First, the fact that within-group related pairs (NFC–NFC) from both populations had lower mean r -values than between-group related pairs (NFC–FC; Table 1) runs counter to the idea that related bears will have similar food-conditioning behavior. Second, although values above 0.0 do indicate a degree of relatedness, the level of relatedness that corresponds to such small r -values does not constitute strong evidence. Finally, we believe the results of the statistical tests are less informative than an evaluation of the frequency distributions (Fig. 1) and estimates of effect size between categories (Table 1; Anderson et al. 2001). In this light, the mean r -values were all close to 0 with relatively small differences between them. We believe the statistical significance is more a product of the large sample sizes than a biological indicator.

It is possible that our results were spurious because we incorrectly categorized individual bears as either FC or NFC. However, we believe that the categorizations were highly reliable, given the in-depth knowledge of bears in each population (Beckmann and Berger 2003; Matthews et al. 2006). Most bears in both populations were easily classified as FC or NFC and remained in these classifications for the duration of 4 years of study. It is also possible our results were spurious because of inherent error in r -values that lead to incorrect classification of 1st-order relatives and reduced the power to detect differences between groups. We acknowledged this possibility of classification error by performing an analysis in which we treated r -values as a continuous variable, which minimized the impact of incorrect classification of 1st-order relatives.

An important factor to consider when interpreting our results is the panmictic spatial genetic structure of populations of black bears due in large part to the dispersal and breeding patterns of male bears (Beecham and Rohlman 1994; Pelton 2003; Rogers 1977). Even if females and their offspring shared learned behaviors, male-mediated gene flow could mask our abilities to detect the link between mother and offspring by homogenizing F_{ST} values between groups (analysis 1) and maintaining distributions of r -values centered around 0 (analysis 4). However, we maintain that the data from the mother–offspring pairings are compelling evidence that FC behavior is acquired through a variety of mechanisms, not just via inheritance or mother–offspring learning.

Black bear cubs likely learn a great deal about foraging during the time they spend under maternal care (Galef and Giraldeau 2001), so why didn't food-conditioning behavior partition along related lineages? One possibility is that the development of FC behavior in black bears is strongly influenced by asocial learning (Galef and Whiskin 2001). Thus, the acquisition of FC behavior could reflect information learned later in life, independently of parents and other bears (Laland 2004). This explanation infers that, for opportunistic species such as black bears, learning to consume anthropogenic food is not

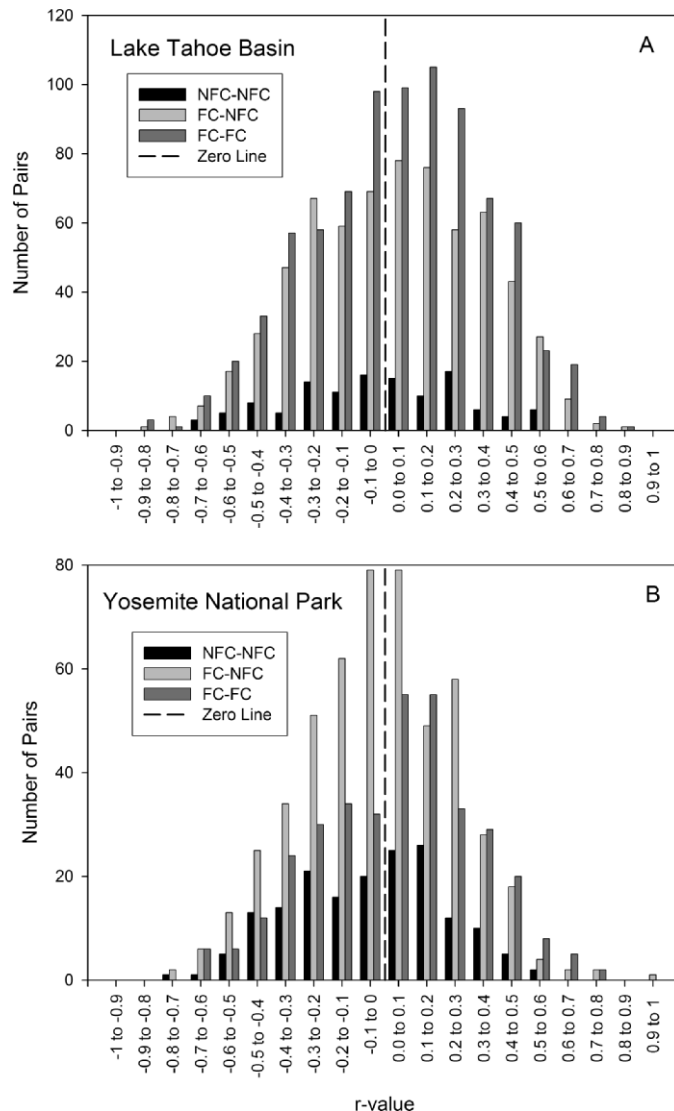


FIG. 1.—Frequency distribution of r -values from all possible pairings of black bears (*Ursus americanus*) labeled as either food conditioned or non-food conditioned (NFC–NFC, FC–FC, and NFC–FC) at A) Lake Tahoe Basin and B) Yosemite National Park.

a behavior that is difficult to acquire, but rather a modification of behavior useful for foraging in natural conditions. Under this scenario, external circumstances such as abundance of natural food sources (McCarthy and Seavoy 1994), relative availability of anthropogenic food sources, and dominance social interactions with other bears (Beckmann and Berger 2003; Galef 2004) would be important aspects that influence the development of FC behavior in bears. The highly skewed sex and age ratios in FC bears from LTB (85% of FC bears from LTB were adult males) implied that social dominance, dispersal, and other ecological factors may have influenced the manifestation of this behavior.

Other explanations involve the influence of humans on the population dynamics and learning processes of bears. For example, a low recruitment rate of cubs among urban bears could have prevented the transfer of behaviors between generations.

Beckmann et al. (2004) documented almost an 85% mortality rate among urban cubs < 16 months of age at the LTB study site. However, the same mortality due to anthropogenic causes was not documented at the YNP study site, casting doubt on the idea that lack of recruitment explains our results. However, at both study sites all FC bears were subjected to aversive conditioning and it is possible that these techniques could have an effect on the dispersal patterns and or behavior of FC cubs.

Finally, although black bears are considered solitary, they do not live completely isolated from other bears; therefore, it also is appropriate to consider social learning among unrelated individuals as an explanation for our results. It is possible that interactions between unrelated bears offered substantial opportunity for learning and were more prevalent than believed. It is also possible that communication among individuals is more complex than currently understood and that chemical cues or physical markings convey information that influences the behavior and opportunities for learning of other bears.

Examination of our data does not refute the concept that bears make additions to their behavioral repertoires by observing relatives or as a result of genetic inheritance, but it does refute the idea that the acquisition of food-conditioning behavior is based primarily on genetic transfer of behavior via parents or social learning between mother and offspring. Whether this pattern holds true for other types of behavior in black bears is unknown, but considering the great adaptability of black bears it is unlikely that any behavior that has application in a diversity of environmental conditions and across a broad geographical range would result in a distinct genetic lineage. However, if a behavior is learned that has narrow application and confers a strong fitness advantage, then there may be more potential for that behavior to lead to distinct genetic lineages. An example might be the situation where individual bears have learned to swim across large expanses (up to 16 km) of ocean to forage on rich sources of food found on islands (Gilbert 1999). Assuming that swimming to distant islands is a behavior that is difficult to learn, it seems more probable that this behavior could be transferred from mother to offspring and lead to a distinct genetic lineage.

In contrast to our results, Meagher and Fowler (1989) reported that adult female grizzly bears classified as “problem” bears contributed only “problem” offspring to the population. The discrepancy could result from incomplete information being reported from their system; the number of nonproblem females that contributed problem offspring and the number of problem females that contributed nonproblem offspring were not reported (Meagher and Fowler 1989). This additional information would have indicated if bears develop food-conditioning behavior regardless of the behavior of their mothers. The discrepancy could also reflect differences between study areas (e.g., ecological conditions), abundance of alternative food during time frames of the study, juvenile dispersal, or behavioral ontogeny and plasticity among populations or species. If different genetic or learning mechanisms operate under different ecological conditions, bears experiencing differing conditions may yield results that differ from ours.

Because of the type of behavior that we studied, our results have important implications for biologists that manage conflict between bears and humans. Our results indicate that most bears are capable of learning to use human food independently of their mothers. Other studies have shown that once a bear is habituated to anthropogenic resources it tends to return to them with regularity (Beckmann et al. 2004; McCarthy and Seavoy 1994). Thus, management strategies that remove problem individuals to eliminate the transfer of behavior between mother and cubs likely will have only limited effect as long as human food sources remain available for bears. A better strategy probably involves preventing bears from learning to use human food sources by eliminating or protecting these food sources so bears are not able to become food conditioned (Creachbaum et al. 1998; Matthews et al. 2006; McCarthy and Seavoy 1994).

The development of food-conditioning behavior has not been rigorously studied in free-ranging bears. We examined this behavior by analyzing genetic relatedness in relation to learning in a solitary species. We presented indirect (based on relatedness among bears) and direct (based on maternity) evidence that bears do not always follow behavioral patterns of close relatives. Given the difficulties of studying behavior using genetic approaches in free-ranging animals, long-term studies tracking the fate of all offspring of mothers in different behavioral categories would be particularly informative. Also, studies focusing on how bears assimilate information, and what constitutes an opportunity for learning, would shed light on how and under what circumstances free-ranging bears develop and retain specific behaviors.

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